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GEOGRAPHIC VARIATION IN THE INSULATIVE QUALITIES OF NESTS OF THE NORTHERN ORIOLE

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There is considerable evidence for the adaptive nature of nesting habits in birds. Horvath (1964) demonstrated intraspecific variation in the nest placement between first and second broods in the Rufous Hummingbird (*Selasphorus rufus*), and related the differences to temperature. Adults of many species shield young from direct sunlight (e.g., Gabrielson 1913, Howell 1942, Davis 1960), dissipate heat through evaporative cooling (Bartholomew 1966), or construct bulkier, "warmer," nests in colder regions (Schaefer 1953, Corley-Smith 1969, Calder 1973). The time spent incubating is also reduced with increasing ambient temperature (see Kendeigh [1952] for a summary of this literature). But, I know of no previous study that has measured interpopulational variation within a species in the insulative qualities of nests under controlled laboratory conditions.

Audubon (1842) noted that nests of the Baltimore Oriole (*Icterus g. galbula*) in Louisiana were more loosely woven than those of orioles nesting farther north. This loose weave presumably facilitated the dissipation of heat from nestling orioles in the warmer clime. His observation, and the hypothesis (Rising 1969, 1970) that a combination of differential heat tolerance and nest-building strategies might ultimately limit the ranges of the eastern "Baltimore" (*Icterus g. galbula*) and western "Bullock's" (*I. g. bullockii*) orioles—now collectively called the Northern Oriole—stimulated me to investigate the interpopulational variation in the nest-building of these birds (Schaefer 1974). I have previously reported (Schaefer 1976) on variation in the placement and structure of nests of these orioles, and herewith report my findings on variation in the relative insulative qualities of the nests.

STUDY AREA AND METHODS

I collected 263 nests from 15 sites in the Great Plains region of the United States, and from 3 sites in Quebec and Ontario (Table 1). In the Great Plains most Northern Orioles from Colorado, New Mexico, western Texas, and extreme western Kansas and Oklahoma are Bullock's, whereas those from eastern Kansas, Nebraska and Oklahoma are Baltimore. In a "hybrid-zone" (Fig. 1) separating these phenotypes the majority of birds are variously intermediate between the 2 types.

Nests were collected in the fall of 1972 and 1973. Only nests from the current nesting season, identified by attachments of recent twig growth, were taken. Data from localities sampled in both years were pooled because no significant differences between the years were found (Schaefer 1974).

TABLE 1

MEAN NEST CUP TEMPERATURES (°C) AND SE FOR INFRARED (IR) AND ULTRAVIOLET (UV) CONDITIONS AFTER 5 AND 15 MIN EXPOSURE[a]

S[b] locality	Phenotype[c]	N	IR 5 min	IR 15 min	UV 5 min	UV 15 min
			$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE
Russell Springs, Ks.[d]	×	5	1.1 ± 0.2	1.6 ± 0.3	0.8 ± 0.1	1.1 ± 0.4
Protection, Ks.[d]	Ba	18	1.1 ± 0.2	0.6 ± 0.4	0.8 ± 0.1	0.6 ± 0.3
Hugoton, Ks.	Bu	7	1.0 ± 0.4	1.6 ± 0.4	0.7 ± 0.2	0.3 ± 0.4
Elm Creek, Neb.[d]	Ba	9	0.9 ± 0.2	−0.2 ± 0.6	0.8 ± 0.1	−0.2 ± 0.3
Meade, Ks.[d]	×	19	0.9 ± 0.1	1.2 ± 0.3	0.6 ± 0.1	0.6 ± 0.2
Sutherland, Neb.[d]	Ba	9	0.9 ± 0.2	0.8 ± 0.7	0.8 ± 0.1	0.9 ± 0.5
Elkhart, Ks.[d]	Bu	11	0.9 ± 0.2	1.2 ± 0.3	0.7 ± 0.1	0.1 ± 0.3
Guthrie, Tex.	Bu	16	0.7 ± 0.1	0.8 ± 0.4	0.5 ± 0.1	−0.1 ± 0.4
Clarendon, Tex.	Bu	25	0.7 ± 0.1	0.7 ± 0.3	0.6 ± 0.1	−0.2 ± 0.2
Utica, Ks.[d]	Ba	5	0.6 ± 0.3	0.7 ± 0.5	0.4 ± 0.2	0.5 ± 0.5
Big Springs, Neb.[d]	×	6	0.4 ± 0.4	−0.2 ± 0.6	0.5 ± 0.2	0.6 ± 0.3
Crook, Colo.	Bu	14	0.4 ± 0.2	0.8 ± 0.4	0.4 ± 0.1	0.0 ± 0.2
Laval, Que.	Ba	6	0.3 ± 0.2	0.1 ± 0.5	0.4 ± 0.2	0.1 ± 0.3
Campbellville, Ont.	Ba	28	0.3 ± 0.1	−0.2 ± 0.3	0.4 ± 0.1	−0.2 ± 0.2
Channing, Tex.	Bu	28	0.3 ± 0.1	0.4 ± 0.3	0.1 ± 0.1	−0.8 ± 0.2
Kenton, Okla.	Bu	23	0.2 ± 0.1	1.3 ± 0.4	0.1 ± 0.1	0.3 ± 0.2
Pickering, Ont.	Ba	13	0.2 ± 0.1	0.1 ± 0.5	0.3 ± 0.1	−0.4 ± 0.3
Weskan, Ks.	Bu	12	0.2 ± 0.2	0.4 ± 0.5	0.2 ± 0.2	−0.8 ± 0.4

[a] Temperatures are expressed as the difference between the experimental and control nests (minus indicates that the experimental nest heated more than the control).
[b] Results of SS-STP analysis for IR 5 min (see text).
[c] Ba = Baltimore Oriole; Bu = Bullock's Oriole; × = hybrid-zone.
[d] Denotes plains Baltimore Oriole or hybrid-zone locality.

The relative insulative qualities of each nest were assessed in a chamber made of plywood (122 × 47 × 76 cm; see Fig. 2), which prevented disturbances in the laboratory from influencing the results. A randomly chosen nest (from Protection, Kansas) was used as a standard. All other nests were tested against it twice, first with a 275 watt General Electric sunlamp (1.5% ultraviolet radiation, 2.7% visible, 95.8% infrared), then with a 250 watt G.E. brooder bulb (0.3% ultraviolet, 4.9% visible, and 94.8% infrared). The 2 tests are referred to as the "UV" and "IR," respectively.

Two different lamps were used because the degree to which nest characteristics (e.g., color, thickness) influence nest temperature depends on the wavelengths of light to which the nest is exposed. The spectra were deliberately chosen to be primarily in the infrared. It seemed that heating of the nest interior would most likely occur from this form of radiant energy. My purpose was to exaggerate the infrared to detect any experimentally determined trends and override large inaccuracies in the procedure which may occur.

I inserted a Philips thermistor (resistance of 1500 ohms at 20°C) through the bottom of each nest and fixed it at 2 cm above the bottom of the nest cup. The thermistors were connected by lamp cord leads to a Wheatstone bridge circuit attached to a Yellow Springs

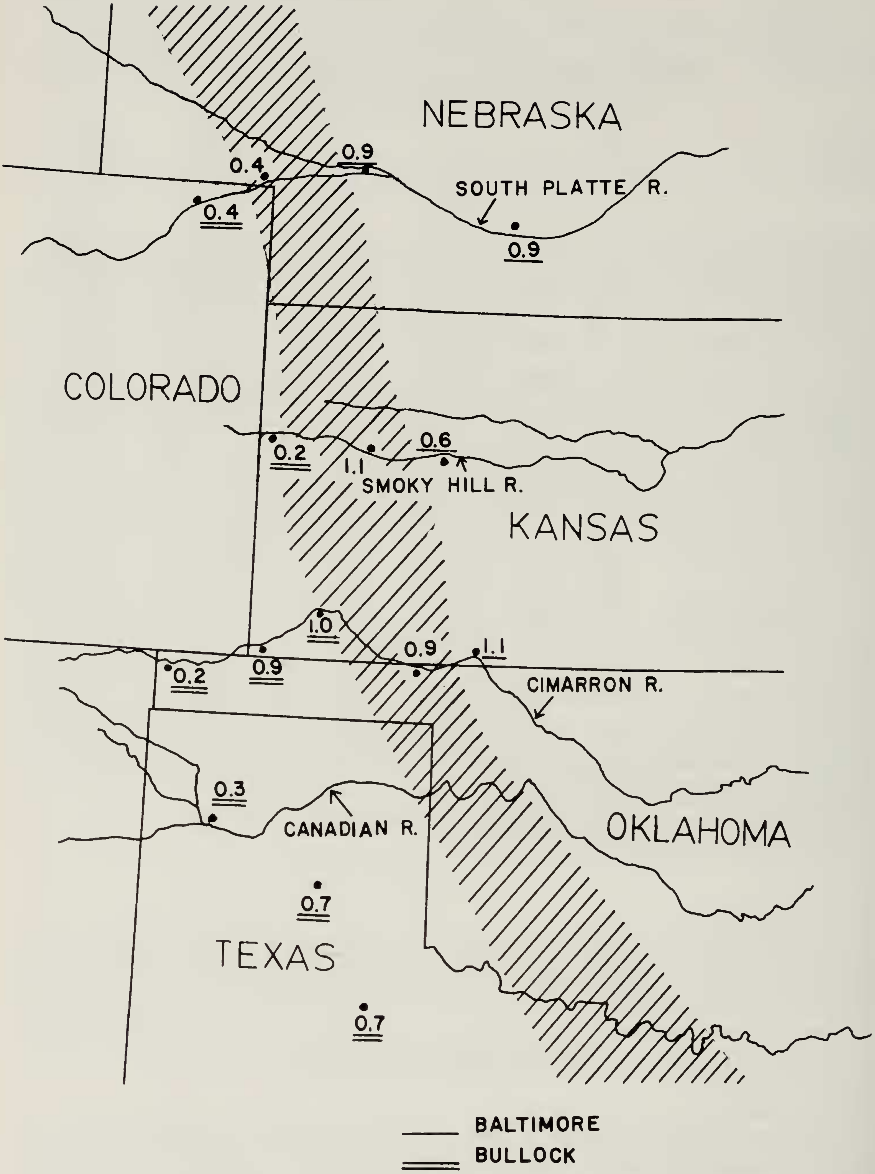

FIG. 1. Map of the central Great Plains showing the sample sites and the experimental values (°C) obtained for the relative insulative qualities of the nests in the IR 5 min experiment. The shaded area approximates the Baltimore-Bullock's oriole hybrid-zone. Localities where the orioles are phenotypically Baltimore are underlined once, Bullock's twice and hybrid-zone not underlined (based on Rising [1970]). Laval, Quebec, and Campbellville and Pickering, Ontario, are not on the map. The experimental values obtained for these localities are 0.3°, 0.3° and 0.2°C, respectively.

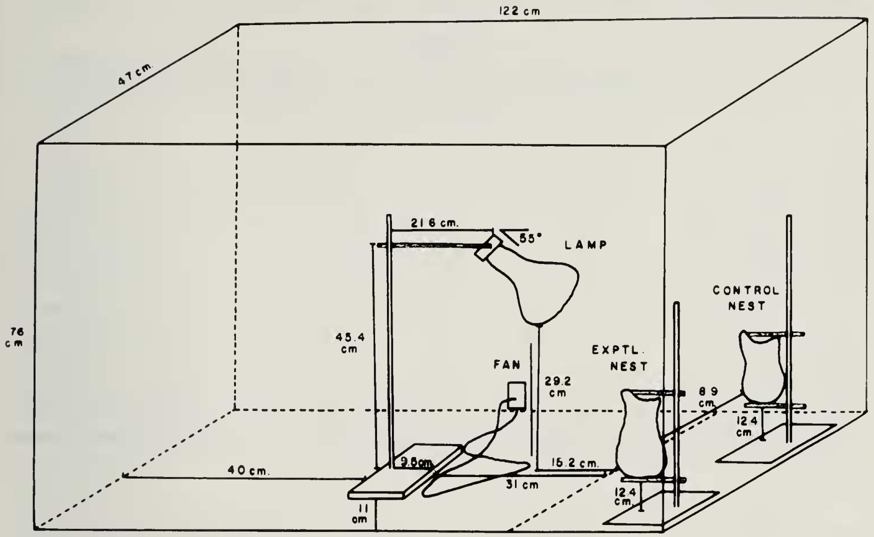

FIG. 2. Schematic diagram of the experimental apparatus used to determine the relative insulative qualities of oriole nests.

Instrument Co. chart recorder. The Wheatstone bridge measured the difference in temperature between the standard and experimental nests.

Temperatures were monitored for 15 min. For the first 5 min a fan within the test chamber provided a turbulent air flow of 6.4–9.6 km/h (measured with a hand-held wind meter). This gave a rough measure of how the nest might be cooled by wind.

Experimental nests were tested in a random order to circumvent possible biases due to changes in experimental conditions between runs. Such biases would mainly originate from the lamps, since intensities and wavelengths of the light emitted depend on usage (Product Manager, Canadian General Electric Co. Ltd., Toronto). Additionally, the standard nest may have been slightly bleached by the lamps, although no visible change in color was noted.

Each nest was placed at a fixed distance from the standard nest, fan and lamp (Fig. 2). The orientation of the experimental nest was standardized by facing the longest attachment closest to the fan and lamp.

RESULTS

Table 1 gives the sample sizes, means and standard errors for the temperature differences between the experimental nests and the standard by locality. The localities are arranged in order of increasing insulation for the IR 5 min condition. The cooler the mean nest temperatures were in relation to the standard nest, the better the nests were insulated from the external experimental source of radiation. Thus, the more negative the number, the more poorly the nests were insulated, and the more positive the value, the better the nests were insulated.

A Model II analysis of variance indicated significant ($P \leq 0.05$) differ-

TABLE 2

MEAN NEST CUP TEMPERATURES (°C) FOR INFRARED (IR) AND ULTRAVIOLET (UV) CONDITIONS AFTER 5 AND 15 MIN EXPOSURE FOR THE LOCALITIES (FROM TABLE 1) GROUPED INTO MAJOR TAXA AND REGIONS[a]

Grouping	No. localities	IR 5 min	IR 15 min	UV 5 min	UV 15 min
Canadian Baltimore	3	0.3	0.0	0.4	−0.2
Plains Baltimore	4	0.9	0.5	0.7	0.5
Hybrid-zone	3	0.8	0.9	0.6	0.8
Texas Bullock's	3	0.6	0.6	0.4	−0.4
Other Bullock's	5	0.5	1.1	0.4	0.0
All Bullock's	8	0.6	0.9	0.4	−0.2
All Baltimore	7	0.6	0.3	0.6	0.2

[a] Temperatures are expressed as the difference between the experimental and control nests (minus indicates that the experimental nest heated more than the control).

ences among localities (i.e., data from nests taken at different geographic sites) in the UV 5 min, UV 15 min and IR 5 min conditions. In each case, SS-STP (sum of squares simultaneous test procedure) (Sokal and Rohlf 1969) *a posteriori* tests showed that only 2 or 3 localities at one extreme were excluded from a statistically homogeneous set of localities that included those at the opposite extreme. Some of the data were significantly skewed with heterogeneity of variance so Kruskal-Wallis tests were also used. There was agreement in the results between the parametric and nonparametric methods of analysis.

The localities were also grouped as Baltimore, hybrid-zone, or Bullock's orioles according to the average index values of the birds for the localities given in Rising (1970:328). An average value greater than 24.5 (cf. a maximum of 28) was arbitrarily taken to be Bullock's Oriole, less than 4.7 = Baltimore Oriole and between 4.8 and 24.4 = hybrids. Baltimore Oriole nests were found to be significantly less-well insulated than hybrid-zone and Bullock's Oriole nests in the IR 15 min condition. Hybrid-zone nests were cooler (better insulated) than Bullock's Oriole nests in the UV 5 and 15 min conditions (SS-STP). A map showing the distribution of the experimental values in the Great Plains for IR 5 min is presented in Fig. 1.

Table 2 shows the experimental values for the localities when they are grouped into categories of Canadian Baltimore, plains Baltimore, hybrid-zone, Texas Bullock's and other Bullock's orioles. Notice that the plains Baltimore and hybrid-zone oriole localities have the highest values in each condition except IR 15 min. Also notice that Canadian Baltimore Oriole nests have lower values than plains Baltimore Oriole nests (they heat up more when exposed to external radiation because they are less-well insulated).

TABLE 3

CORRELATION COEFFICIENTS OBTAINED BETWEEN THE RELATIVE INSULATIVE QUALITIES OF NESTS AND MAY AND JUNE WEATHER[a]

	May				June			
Character	IR 5 min	IR 15 min	UV 5 min	UV 15 min	IR 5 min	IR 15 min	UV 5 min	UV 15 min
Total precipitation	0.57*	0.24	0.44	0.31	0.33	−0.25	0.35	0.09
Mean temperature	0.58*	0.59*	0.29	0.16	0.60*	0.62**	0.29	0.20
Minimum daily temperature	0.62**	0.47*	0.38	0.08	0.65**	0.52*	0.41	0.19
Maximum daily temperature	0.34	0.34	0.15	0.13	0.50*	0.48*	0.24	0.18
Highest temperature	0.73**	0.37	0.56*	0.15	0.69**	0.42	0.53*	0.28
Lowest temperature	0.19	0.20	0.06	−0.11	0.41	0.49*	0.24	0.10

[a] r, df = 16.
* $P \leq 0.05$.
** $P \leq 0.01$.

Table 3 shows the Pearson product-moment correlation coefficients (r) obtained between the relative insulative qualities of the nests and each of 6 weather variables which may contribute to heat stress in orioles (10-year or more averages based on summaries obtained from the Weather Bureau, U.S. Dept. Commerce and from Environment Canada). Only May and June were considered because they are the months when nest construction and incubation usually occur in orioles.

Nest cup temperatures after 5 min with a turbulent air flow over the nests gave the largest number of significant correlations with both May and June weather. The highest correlation ($r = 0.73$, df = 16) is between the highest temperature for May and the IR 5 min condition, i.e., orioles build well-insulated nests in places with high May temperatures. Nests from localities where the ambient temperatures were higher remained cooler in the experiments.

The IR conditions produced all but one of the significant correlations for each month. Only the highest temperatures for each month were significantly correlated with the UV results. The total precipitation correlated with the relative insulative qualities of the nests for the localities only for the month of May for IR 5 min.

DISCUSSION AND CONCLUSIONS

Kendeigh (1963) found that there was a significant positive correlation between nest and air temperatures in the House Wren (*Troglodytes aedon*). He also found that the temperatures inside nests sometimes exceed air temperatures, especially if the nest was exposed to the sun. Indeed, he mentioned that nest temperatures may be sufficiently higher than optimal incubation temperatures for long enough periods to injure or kill embryos. Even nests shaded throughout most of the day can be exposed to brief periods of damaging sunlight. In areas where ambient temperatures are high any heat perturbations to the nest could be lethal to developing embryos.

Laboratory birds of Baltimore Oriole phenotype seem to be more sensitive to high temperatures than do those of the Bullock's Oriole phenotype (Rising 1969). The hybrid-zone in the Great Plains delimits the western edge of the range of the Baltimore Oriole, a region where it would be exposed to the hottest temperatures it would normally encounter. I earlier determined (Schaefer 1974) that while oriole nest temperatures were significantly correlated with ambient temperatures, they were also significantly lower. However, sometimes nest temperatures exceeded ambient temperatures, and once I recorded a nest temperature of 41°C within a nest *in situ* in Kansas (ambient temperature = 38°C). Thus, Baltimore Orioles may undergo heat stress in the Great Plains and may build better insulated nests. The generally thicker (pers. obs.) nests of Great Plains Baltimore Orioles can prevent the contents from heating up if there is an external source of radiation (as in the case of my experiments) coming from the sun. Most of the trees in the Great Plains are young cottonwoods (*Populus* spp.), which allow the sun to penetrate through the canopy for short periods. In Louisiana, where Audubon (1842) noted that Baltimore Oriole nests were thinner, the orioles may successfully shade their nests but still face a high ambient temperature. In such a region, a thinner nest may be more efficient in keeping the interior cool.

Baltimore Orioles may place their nests on the shaded sides of trees to keep them out of the sun for at least part of the day. However, I (Schaefer 1976) found that in those localities where orioles did seem to place their nests on a particular side of a tree, the relationship seemed to be more with wind (leeward sides were preferred), rather than sunlight. Orioles in the Great Plains may be prevented from nesting on the shaded sides of trees because of strong prevailing winds.

A bulky nest construction helps to keep heat produced by external radiation on the surface of the nest. The heat can then be dissipated by wind (note that the highest correlations obtained between the insulative qualities of nests and locality temperatures occurred when the fan was blowing on the nests [Table 3]). Thus, the interior of a bulky nest may remain cooler than one which is thinner.

The absence of many significant correlations between the UV experimental values and weather for the localities could be due to experimental error. The overall relationships were similar to those of the IR conditions

(Table 2: plains Baltimore Oriole highest, hybrid-zone next, then the Canadian Baltimore and plains Bullock's orioles).

Alternatively, the slightly greater amount of visible radiation in the IR conditions could have exaggerated the differences in the relative insulative qualities of the nests. Natural solar radiation on the earth's surface is 10% UV, 45% visible and 45% IR (Reifsnyder and Lull 1965). Thus, the larger amounts of visible energy in natural solar radiation may make the relative insulative qualities of oriole nests more responsive to nest color. The larger amounts of visible energy in the IR experiments could contribute to explaining why there were more significant correlations with weather with the IR values and fewer for UV. Plains Baltimore Oriole nests are notably lighter than those from Canada. Plains nests may be bleached by the sun more than nests in Canada and may become better insulated against heating as a result.

Total precipitation for the localities correlated significantly only between May and IR 5 min. Possibly, decreased precipitation could contribute to evapotranspiration stress, but the relationship should have been negative and not positive as found. The significance may have been a chance event, or perhaps precipitation is a covariable of locality temperatures which showed a much stronger relationship with the relative insulative qualities of the nests.

SUMMARY

The relative insulative qualities of 263 nests from 18 localities of the Northern Oriole were determined experimentally. Differences in the relative insulative qualities of the nests showed trends of geographic variation. Canadian Baltimore and Bullock's orioles' nests are less resistant to heating by an external source of radiant energy than nests of Baltimore Orioles in the Great Plains and Northern Oriole nests from the Baltimore-Bullock's oriole hybrid-zone. The relative insulative qualities of the nests were significantly correlated with local temperatures.

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LITERATURE CITED

AUDUBON, J. J. 1842. The birds of America. Dover Edition, 1967. Vol. 4. Dover Publications Inc., New York, New York.

BARTHOLOMEW, G. A. 1966. The role of behavior in the temperature regulation of the Masked Booby. Condor 68:523–535.

CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

CORLEY-SMITH, G. H. 1969. A high altitude hummingbird on the volcano Cotopaxi. Ibis 111:11–32.

DAVIS, J. 1960. Nesting behavior of the Rufous-sided Towhee in coastal California. Condor 62:434–456.

GABRIELSON, I. N. 1913. Nest life of the Catbird. Wilson Bull. 25:166–187.

HORVATH, O. 1964. Seasonal differences in Rufous Hummingbird nest height and their relation to nest climate. Ecology 45:235–241.

HOWELL, J. C. 1942. Notes on the nesting habits of the Robin. Am. Midl. Nat. 28:529–604.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 12.

———. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. Pp. 884–904 *in* Proc. XXIII Int. Ornithol. Congr.

REIFSNYDER, W. E. AND H. W. LULL. 1965. Radiant energy in relation to forests. U.S. Dept. Agric., Forest Services, Tech. Bull. No. 1344.

RISING, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock's orioles. Comp. Biochem. Physiol. 31:915–925.

———. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.

SCHAEFER, E. 1953. Contribution to the life history of the Swallow-tanager. Auk 70:403–460.

SCHAEFER, V. H. 1974. Geographic variation in the placement and structure of the nests of three taxa of North American orioles. M.Sc. thesis, Univ. Toronto, Toronto, Ontario.

———. 1976. Geographic variation in the placement and structure of oriole nests. Condor 78:443–448.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, California.

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